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Isolated trees as nuclei of regeneration in tropical pastures: testing the importance of niche-based and landscape factors

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Abstract

Questions: Our study tests the relative importance of different attributes of isolated trees in explaining the properties of the regeneration assemblage beneath their crowns to evaluate their effect on the composition of early successional stages and understand the processes underlying this effect. We asked: (1) does the regeneration assemblage contain a high proportion of individuals conspecific with the isolated tree; (2) how does the landscape surrounding an isolated tree influence the properties of the regeneration assemblage; and (3) what is the respective importance of structural variables and functional traits of isolated trees for their influence on the properties of the regeneration assemblage?

Location: Three pasture sites in Guanacaste Province, a tropical seasonally dry area, Costa Rica.

Methods: Ninety isolated trees were characterized by their position in the landscape relative to patches of trees, individual structural variables related to tree and crown size, and species functional traits. The assemblage of woody plants regenerating under their crowns was characterised by number of individuals and species, and taxonomic and functional composition. To understand the mechanisms underlying the facilitative effect of isolated trees on regeneration, correlations between their attributes and properties of the regeneration assemblage were assessed.

Results: We found that a low proportion of regenerating individuals were conspecific with the isolated trees beneath which they have established. Landscape factors influenced the regeneration but their

effects were site dependent. The attributes of isolated trees correlated well with the functional composition of the regeneration assemblage: their structure and phenological habits with traits associated with drought tolerance, and their dispersal syndrome with the dispersal syndrome of the regeneration assemblage. However, isolated tree attributes correlated poorly with the regeneration assemblage's taxonomic composition.

Conclusions: Our study shows that an approach based on functional composition can provide a better understanding of community assembly mechanisms than does a taxonomic approach. Two main mechanisms are suggested to explain the influence of isolated trees on the regeneration assemblage: modification of micro-scale environmental conditions (shade and moisture) and influence on dispersal agents. The effect of attributes of isolated trees on the properties of the regeneration assemblage predicts a long-term legacy of the early stages of succession.

Keywords

Biodiversity; Community assembly; Costa Rica; Environmental filtering; Facilitation; Plant functional traits; Regeneration; Secondary succession; Seed dispersal; Tropical dry forest

Nomenclature

The Plant List (http://www.theplantlist.org/; accessed on 15 Jan 2015)

Abbreviations

TDF = Tropical Dry Forests; the abbreviations for the attributes of isolated trees are given in Appendix S1

Running head

Isolated trees as nuclei of regeneration

Introduction

Conversion of forests into agricultural land is one of the major anthropogenic pressures on tropical forests (FAO 2012). However, socio-economic changes and restoration efforts can reverse this trend and allow secondary forest establishment (Calvo-Alvarado et al. 2009). When cattle farming is abandoned, isolated trees in pastures can promote the natural regeneration of woody forest species and therefore the early stages of succession (Holl et al. 2000). The positive role of isolated trees as nuclei of regeneration in abandoned pastures has long been evidenced in tropical wet forest zones (Guevara et al. 1986, 1992; Slocum & Horvitz 2000; Carrière et al. 2002; Schlawin & Zahawi 2008) and to a lesser extent in tropical dry forest zones (Janzen 1988, 2002; Castillo-Nunez et al. 2011; Griscom & Ashton 2011). The mechanisms that underlie the facilitative effects of isolated trees are thought to be mainly facilitation of seed dispersal by attraction of dispersal agents (Guevara et al. 1986) and facilitation of germination and seedling establishment by amelioration of microclimate (Duarte et al. 2010).

Several studies suggest that isolated trees may differ in their positive effect on regeneration: their attributes can influence the number of individuals and species (Guevara et al. 1986; Slocum & Horvitz 2000; Slocum 2001) and the taxonomic composition (Duarte et al. 2010) of the assemblage of woody plants establishing under their crown (*i.e.* the regeneration assemblage). Unfortunately, most of these studies were conducted on a very limited number of individuals and species of isolated trees. This leads to a high risk of bias, which makes the understanding of general trends difficult. Moreover, most of these studies characterize the regeneration assemblage only in terms of taxonomic composition and diversity (Duarte et al. 2010; Slocum & Horvitz 2000; Slocum 2001), whereas its functional composition has only been characterised by the seed dispersal syndrome (Guevara et al. 1992). Considering other functional traits of regenerating plants, such as those associated with environmental requirements, could provide a better understanding of the effects of isolated trees on the composition of the regeneration assemblage. Young plants have particularly specific environmental requirements: trees have been found to be more strongly adapted (through functional trait values) to their regeneration niche (*sensu* Poorter (2007)) than their adult niche (Poorter 2007).

Besides these niche-based processes, factors linked to a tree's location relative to surrounding tree patches (referred to here as landscape factors) are also expected to influence regeneration since they are generally linked to seed availability and dispersal (Chazdon 2014). It is important in advancing ecological theory to investigate whether or not these landscape factors act in a similar way across regenerating species, independently of a species' ecological requirements. If they do, they can then be considered as neutral (*sensu* Hubbell (2001)), but should not be considered stochastic if they are

explainable and predictable (Lebrija-Trejos et al. 2010a). However, if the influence of landscape factors varies with the identity of species or their functional type, then it is non-neutral.

The processes underlying the effect of isolated trees on regeneration remain poorly understood and more studies on the hierarchy of importance of different attributes of isolated trees and of landscape factors that promote this effect (such as Duarte et al. (2010)) are needed (Peterson et al. 2014). This is especially true in tropical dry forests, where seasonal water limitation represents a major constraint to regeneration (Maass & Burgos 2011) and the balance of tree seed dispersal syndromes (Vieira & Scariot 2006) has led to the prediction that the effect of isolated trees on regeneration should be different from that in moist forests. Since regeneration under trees in pastures constitutes a very early step in forest recovery, evaluating the importance of attributes of isolated trees for the structuring of the regeneration assemblage will enable assessment of the importance of the legacy of the initial tree composition (Egler 1954), and of the deterministic and predictable character of succession.

Improved understanding of the factors explaining the positive influence of isolated trees on regeneration also has obvious applications in ecological restoration of tropical dry forests, a globally threatened biome (Miles et al. 2006). Important restoration opportunities are provided by the recent trend of abandonment of livestock production in this climatic zone (Calvo-Alvarado et al. 2009) and growing interest in the role of secondary forests in biodiversity conservation (Chazdon et al. 2009). Knowledge about these early-stage regeneration mechanisms can inform practitioners about which traits to use in the selection of species for the role of nurse trees for restoration, especially when using techniques based on the nucleation model of succession (Yarranton & Morrison 1974), which are receiving increasing attention (Rey Benayas et al. 2008; Corbin & Holl 2012).

Our study investigates the factors structuring woody plant regeneration under isolated pasture trees in dry tropical areas. We aim to test the importance of landscape factors and of the attributes of isolated trees acting at a more local scale (individual structural variables and species functional traits) in explaining the properties of the woody plant regeneration assemblage beneath their crowns, by surveying the assemblage under a large sample of isolated trees in active pasture sites in Costa Rica. We ask the following questions: (1) does the regeneration assemblage contain a high proportion of individuals of the same species as the isolated tree beneath whose crown it occurs? Because most tree seeds are dispersed short distances (up to 200-300 m) from the parent tree in this biome (Janzen 1988), we expect this proportion to be high. However, if the mortality rate of seedlings of the same species as the adult tree is higher than for other species, as predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971), we expect this proportion to be low. (2) Do landscape factors influence the number of individuals and species, the taxonomic composition, and the functional composition of the

regeneration assemblage? If so, what is the most influential landscape factor? We expect landscape factors to be important but do not know over what scale they would have a detectable effect. (3) What is the relative influence of structural variables (e.g. height, crown area) and functional traits of isolated trees on the number of individuals and species, taxonomic composition and functional composition of the early woody regeneration assemblage that occurs beneath their crowns? We predict that the attributes of isolated trees would have two effects: (1) the structural variables and the leaf phenological habit of the isolated trees are expected to influence traits of the regenerating plants linked to resource acquisition (water and light) through their impact on the microenvironment and (2) the seed dispersal syndrome and structure of the isolated trees are expected to act on dispersal of seeds beneath their crowns by attracting dispersal agents.

Methods

Study site and studied trees

The study was conducted in Guanacaste Province, north-western Costa Rica. The climate is characterized by strong rainfall seasonality with a 5-6 mo dry season and > 95% of the ~ 1700-mm mean annual rainfall falling during the May-November wet season (*Instituto Meteorológico Nacional de Costa Rica*, meteorological station of Liberia 10.58^{o} N; 85.53^{o} W, 1977-2012). The original vegetation is tropical dry forest (TDF; Holdridge et al. 1971). Extensive conversion of these forests to pasture land occurred until the 1980s. Since then, forest conservation policies combined with socio-economic changes have resulted in forest recovery (Calvo-Alvarado et al. 2009) across a mosaic of pastures and secondary forests of different ages.

Three active pasture sites located on private lands were studied: Ahogados (10.80^{o} N, 85.54^{o} W), Lamentos (10.74^{o} N, 85.63^{o} W) and Aromal (10.73^{o} N, 85.60^{o} W; Fig. 1). The age of the pastures (i.e. time since conversion) was at least 45 yr. Qualitative data on the past and present land uses of these sites have been obtained from landowners and managers and are reported in Appendix S1. The pastures are flat and crossed by a number of non-permanent streams lined with riparian vegetation.

We selected a high number of individuals and species of isolated trees to minimize the risk of bias due to phylogenetic correlation amongst traits. We used several inclusion criteria for trees: (1) crown not overlapping with the crown of another tree; (2) no substantial part of the crown covered by a liana (so that the effects of trees could be separated from lianas); (3) located in an area with environmental conditions comparable to the rest of the site (areas that had hydromorphic soil or recent burning were excluded). We conducted a pre-survey of all isolated trees in each site and estimated their distance to the nearest tree patch (as defined in the section on attributes of isolated trees below), height and crown radius. We then selected 30 trees per site (90 trees from 30 species in

total) to match the species mix of all trees present in each site and to cover the full range of values for these three estimated variables.

Attributes of isolated trees

Three types of attributes were quantified for each tree: landscape factors, structural variables of the individual tree and functional traits of its species. We calculated the following landscape factors for each tree: distance to the nearest tree patch (*Distance*), and the area of tree patches in buffers of 100 m ($Area_{100}$), 500 m ($Area_{500}$) and 1000 m ($Area_{1000}$) around the focal isolated tree. To do so, we recorded the coordinates of each tree and used two orthophotos to delimit the trees patches, defined as an area ≥ 400 m² with a predominantly closed canopy of mature trees (riparian vegetation was included), in ArcGIS (ESRI, 1999-2009) (see Appendix S1 for details).

We considered the following structural variables for their likely impact of the amount of shade cast by isolated trees, as rigorous measurement of shade was impractical due to its high seasonal dependency: total height (*Height*), height of the bottom of the lowest branch (*Hbranch*), *Crown length*, *Crown area*, *Crown volume*, ratio of crown length : tree height (*RhH*), ratio of crown area : tree height (*RAH*), ratio of crown volume : tree height (*RVolH*), ratio of crown area : crown length (*RAh*) and *Sampling area* delimited by the vertical projection of the tree's crown edge plus a 1-m buffer beyond (details of the measurement and calculation of these variables are provided in Appendix S1).

For the functional traits of isolated trees, three variables were considered. Values of the seed dispersal syndrome (*Dispersal*, two categories: zoochorous *vs* anemochorous and autochorous) and the leaf phenological habit (*Phenology*, two categories: evergreen and semi-deciduous *vs* fully deciduous) of the tree species were obtained from data provided in Powers & Tiffin (2010) supplemented by information obtained from local experts (Roberto Espinoza and Daniel Perez Avilez, pers. comm.). Information on the capacity to fix nitrogen (*N-fixation*) of all Leguminosae species was obtained from Halliday (1984), Sprent & Parsons (2000), Sprent (2005), Wishnie et al. (2007) and Griscom & Ashton (2011).

Although not strictly an attribute of isolated trees, we used *Site* as a variable qualifying isolated trees because *Site* encompasses a range of non-stochastic factors that have not been measured, such as the intensity of grazing, pasture management practices and variation in soil and hydrology.

Survey and properties of the regeneration assemblage

In July 2013, we conducted a survey of the regenerating woody vegetation under each selected isolated tree. We quantified and identified all seedlings, saplings and young adults of trees, tall shrubs (only shrub species that can grow > 2 m height were considered) and woody lianas located in the *Sampling area*. Individuals sprouting from the roots of the trees (as visually assessed by inspecting the

first few centimetres of the tap root) were excluded. The minimum height for a plant to be included was 10 cm, to exclude seedlings germinated in the year of data collection, which have not yet experienced the full annual climatic cycle. We set no upper height limit for inclusion. However, we did not select isolated trees where the relative size of trees with overlapping crowns created any uncertainty about whether the isolated tree established before the woody regeneration located under its crown.

Each species of regenerating woody plant was assigned to one life-form category (trees and shrubs *vs* woody lianas), leaf structural complexity category (simple *vs* compound) and taxonomic category (member of Leguminosae family *vs* not) based on literature (Enquist & Sullivan 2001; Powers & Tiffin 2010) and on-line resources (INBio; http://atta2.inbio.ac.cr and Flora de Nicaragua; http://www.tropicos.org/Project/FN, accessed on 10 Dec 2013). Information of leaf phenological habit (evergreen and semi-deciduous *vs* fully deciduous) and dispersal syndrome (zoochorous *vs* anemochorous and autochorous) was obtained from the same sources as for the species of isolated tree (see Appendix S1 for details on the choice of categories). For trees and shrubs, leaf phenological habit and leaf complexity were selected as traits that indicate a species' drought tolerance and light-capture strategies (Poorter & Markesteijn 2008), although there are some notable exceptions for leaf complexity (e.g. *Guazuma ulmifolia*). These two traits and membership of the Leguminosae family were not considered for lianas because there is no evidence that they relate to plant strategies in the same way as for trees and shrubs. For some species, we were unable to find information on one or more of these traits, but these species never represented more than 0.8% of the individuals found under a tree or 0.05% of the total number of regenerating individuals.

We characterized the assemblage of regenerating individuals occurring under the crown of each sampled isolated tree using the following properties: proportion of conspecifics (individuals of the same species as the tree), number of individuals, number of species, taxonomic composition (at the species level, i.e. number of individuals per species), and functional composition characterized by life form, seed dispersal syndrome, and for individuals of tree and shrub species only, leaf phenological habit, leaf complexity and proportion of individuals from the Leguminosae family. We excluded regenerating individuals of the same species as the isolated tree above from the calculation of all regeneration properties, except the proportion of conspecifics itself. They are likely to originate from seed produced by that tree, which could influence the results related to mechanism of seed dispersal.

Statistical analysis

The influence of the seed dispersal syndrome of isolated trees on the proportion of conspecifics beneath their crowns was tested using a quasi-binomial GLM with a logit link.

To test the influence of each landscape factor on the number of regenerating individuals, their number of species and their functional composition, we performed simple negative binomial and quasi-binomial GLMs to account for over-dispersion. Models were fitted site-by-site and for one landscape factor at a time, to avoid bias due to collinearity between *Site* and landscape factors (Zuur et al. 2010).

To test the relative influence of the attributes of isolated trees on the taxonomic composition of the regeneration assemblage, we used RDA with a Chord transformation. This method computes axes that best explain the variation of the floristic table and expresses each axis as a linear combination of the 17 attributes of isolated trees (Legendre & Gallagher 2001). The continuous attributes were standardized; the absolute values of the canonical coefficients can therefore be used as a measure of the importance of each explanatory variable for each axis (Borcard et al. 2011). The best model was selected using a forward selection and the adjusted R^2 was retrieved following the method of Borcard et al. (2011).

To test the respective influence of the attributes of isolated trees on the number of individuals, the number of species and the functional composition of the regeneration assemblage, we used multiple GLMs. For structural variables of isolated trees, we considered only *Hbranch*, *RAh*, and *RhH*, to avoid bias due to collinearity. For the same reason, we included either (i) *Dispersal* or (ii) *Phenology* and *N-fixation* in each analysis depending on the ecological hypothesis that it was testing. The interactions between *Phenology* and structural variables (*RAh* and *RhH*) were the only ones considered in testing if a potential effect of tree structure could differ between evergreen and deciduous trees, since in TDF leaf phenological habit influences the effect of trees on regeneration (Derroire et al. 2016). We used negative-binomial distributions for count data (number of individuals and number of species) and quasi-binomial GLMs for proportional data (functional composition), to account for over-dispersion. The best models were selected by performing a backward selection based on the Akaike Information Criterion (AIC) for negative-binomial GLMs and on the quasi-AIC (Burnham & Anderson 2002) for quasi-binomial GLMs.

Details of the statistical analyses and a list of the variables considered for each analysis are presented in Appendix S1. All analyses were performed using the environment and language R (R Foundation for Statistical Computing, Vienna, AT) and the packages MASS (Venables & Ripley 2002) and vegan.

Results

We surveyed regeneration of woody plant species in a total *Sampling area* beneath the crowns of isolated trees of 17 089 m² and recorded 6802 individuals (90.7% tree and shrub species; 9.3% lianas),

including individuals conspecific with the isolated tree above. The number of regenerating individuals beneath each isolated tree ranged from 0 to 392 (415 for an outlier tree described in Appendix S3). Details of the regenerating woody plants and isolated trees are provided in Appendices S2 and S3.

The proportion of conspecifics between the isolated trees and the regeneration assemblage beneath their crowns was generally low (mean of 5.6% of regenerating individuals) but varied greatly amongst the trees (from 0 to 58.8%). Of the 90 surveyed trees, 58 (64.4%) had no conspecific regenerating individuals and only eight (8.8%), comprising five tree species, had more than 25%. The proportion of conspecifics was not dependent on the seed dispersal syndrome of the tree (GLM $p = 0.876$).

All the properties of the regeneration assemblage (except life form) were correlated with some of the included landscape factors but these correlations varied with *Site* (Table 1). The number of individuals in the regeneration assemblage decreased with increasing *Distance*, and the number of both individuals and species increased with increasing $Area_{100}$ but not with $Area_{500}$ and $Area_{1000}$. The proportion of individuals of zoochorous species decreased where $Area_{100}$ or $Area_{500}$ increased. The proportion of individuals of compound-leaved species was also generally linked to landscape, increasing with *Distance* and slightly decreasing with $Area_{500}$ and $Area_{1000}$. The proportion of individuals of Leguminosae species also increased with *Distance* and decreased with $Area_{100}$ and $Area_{1000}$.

The 16 attributes of isolated trees were only weakly linked to the taxonomic composition of the regeneration assemblage under their crowns. The overall R^2 of the best model obtained by RDA was 12.84% ($p < 0.001$). This model kept the explanatory variables *Site*, $Area_{100}$, *RhH* and *N-fixation* (Table 2). The canonical coefficients show that *Site* is the most important variable in explaining the three axes retained in the best model.

The selected models explained a high percentage of the deviance of the number of individuals (61.10%) and the number of species (58.16%) in the regeneration assemblage (Fig.2, Table 3, Appendix S4). Both the number of individuals and the number of species increased with *Log Sampling area* and depended on *Site*. There were more regenerating species under evergreen and semi-deciduous than deciduous trees.

Three aspects of the functional composition of the regeneration assemblage were exclusively linked with the structural variables and functional traits of the isolated trees (Fig. 2; Table 3; Appendix S5): a higher proportion of individuals comprising zoochorous species was found under zoochorous trees (overall R^2=11.16%). The proportion of individuals comprising deciduous species was positively correlated with *RhH*, negatively with *Crown area* and was higher under deciduous trees (overall R^2=26.52%). The proportion of individuals comprising compound-leaved species increased with *RhH* (overall R^2=12.30%). The proportion of individuals comprising Leguminosae species increased with

RhH, was lower under N-fixing than under non-N-fixing trees and varied with *Site* (overall R^2=28.96%). The proportion of individuals comprising tree and shrub species was also strongly linked to *Site* (overall R^2=21.97%).

Discussion

Low proportion of conspecificity

We found a low proportion of conspecificity between the isolated trees and the regeneration assemblage beneath their crowns. Moreover, this proportion did not differ significantly between species with different seed dispersal syndromes, suggesting that this low proportion is not likely to result from an event at the dispersal stage. It could be explained by distance and/or density-dependent mortality of regenerating plants close to an adult of the same species, due to high risk of predation and pathogen attack. This hypothesis, first formulated by Janzen (1970) and Connell (1971), has been supported by a high number of experimental studies (Comita et al. 2014). The low proportion of conspecifics predicts a high rate of species replacement, which, together with the high number of species in the regeneration assemblages, supports the importance of isolated trees in early stages of succession (Holl et al. 2000).

The effect of landscape factors is context-dependent

The effect of surrounding tree patches within a buffer distance on the number of individuals and species in the regeneration assemblage was observed at the smallest tested scale (100 m), for one site. This is consistent with the short distance of movement of birds and bats and the short maximum dispersal distances for anemochorous tree species in pasture. Both distance have been found to be generally <200-300 m from the forest edge (Janzen 1988; Estrada et al. 1993; Silva et al. 1996). However, in the other two sites, the number of regenerating individuals was not significantly correlated with any landscape factors. This is consistent with several studies that did not observe a significant effect of distance to the nearest forest on density or richness of the regeneration assemblage (Slocum & Horvitz 2000; Duarte et al. 2010). This suggests the potential importance of other landscape factors untested in our study, such as the direction of the tree patches relative to dominant wind direction (Janzen 2002), or presence of scattered trees or live-fences acting as stepping stones and corridors for disperser birds and bats (Estrada et al. 1993; Chazdon et al. 2011). Although landscape factors are considered to mainly act on seed dispersal limitation, they could also influence environmental conditions (Pejchar et al. 2008). In our study, this latter mechanism may be the best explanation for the decrease in proportion of regenerating individuals comprising species with compound leaves when the area of tree patches within a buffer distance increased, as this trait has

been shown to be associated with dry conditions (Poorter & Markesteijn 2008). Measurement of environmental conditions under isolated trees would be needed to provide direct evidence of the mechanisms by which landscape factors influence regeneration. Nonetheless, the correlations found between landscape factors and functional composition of regenerating communities indicates that the effect of landscape factors are non-neutral (Vellend et al. 2014).

In our study, the effect of site identity on the number of individuals and species in the regeneration assemblage is partly explained by the correlations between site identity and landscape factors: there were more individuals and species in the site with a higher area of tree patches in the vicinity (Fig. 1; Table 3; Appendices S3 and S4). The variable *Site* can also be considered as a proxy for non-measured variables: its effect can be attributed to differences in the composition of the local species pool, even though the sites are never more than 12 km apart. It can also reflect other factors such as past land use, current management (including the effect of cattle), variation in soils, seed predation and insect herbivory, all of which have been shown to be important in controlling the process of secondary succession (Chazdon et al. 2003).

Attributes of isolates trees influence the functional composition of regeneration assemblages

Attributes of the studied isolated trees were clearly linked to the functional composition of the regeneration assemblage beneath their crowns (Table 3; Fig.2), while showing little influence on their taxonomic composition (Table 2). Our results suggest two mechanisms to explain this effect: amelioration of environmental conditions and attraction of seed dispersal agents.

The correlations that we found between the isolated trees' structural variables and leaf phenological habit and the regeneration assemblage's proportion of individuals having traits associated with tolerance of drought and heat (deciduous and compound leaves) (Poorter & Markesteijn 2008), suggest that isolated trees affect regeneration through environmental amelioration, as found by Duarte et al. (2010). An increase in crown area is associated with the casting of more shade beneath the tree crown, and thus a greater amelioration of the air temperature (Rhoades et al. 1998), air humidity and soil moisture micro-environment (Callaway 2007). Evergreen and semi-deciduous isolated trees provide shade during the dry season and are therefore expected to mitigate high temperatures and low air humidity. While the effects of structural variables and leaf phenological habit of isolated trees are likely to interact, our results did not quite show this to be significant ($p = 0.064$ for the interaction of the ratio crown area : crown length and the phenological habit of the isolated tree in the model for regeneration assemblage leaf phenology). Mitigation of harsh environmental conditions is expected to allow individuals of species with traits generally associated with a lower tolerance of drought and heat (simple leaves and evergreen) to establish. Such

positive effects of tree shade are not supported in humid tropical areas (Slocum 2001) where water limitation is not as severe as in the dry tropics.

Seed dispersal syndrome of isolated trees correlated with the proportion of individuals of species with different dispersal syndromes in the regeneration assemblage. Our model predicts almost 1.3 times as many zoochorous individuals regenerating under a zoochorous tree than under an anemochorous tree (Appendix S5). Many studies have reported a higher number of zoochorous species regenerating under isolated trees than in open pasture (Guevara et al. 1986, 1992; Galindo-González et al. 2000; Carrière et al. 2002; Zahawi & Augspurger 2006), which can be attributed to their attraction of seed dispersers: mainly birds (Silva et al. 1996; de la Peña-Domene et al. 2014), but also bats (Galindo-González et al. 2003). However, most studies do not disentangle the attraction of dispersers for perching or foraging. The link that we found between the dispersal syndrom of isolated trees and of woody individuals regenerating beneath their crowns provides good evidence of the importance of attraction for foraging by seed-dispersers. Some studies have found more seeds under zoochorous trees (Slocum & Horvitz 2000; Carrière et al. 2002) but in our case, the total number of seedlings was not correlated with the seed dispersal syndrome of the tree, presumably because of the filtering effects of seed germination and seedling establishment (Howe et al. 2010).

The correlation between the proportion of Leguminosae individuals and the attributes of isolated trees (N-fixation capacity and ratio crown length : tree height) that we found supports the designation of Leguminosae as a distinct functional group in TDF with a distinct response to small-scale variation in environmental conditions relative to competing plants of non-Leguminosae species. In the same region, Powers & Tiffin (2010) found that the values of leaf C and N content, wood density and leaf stoichiometry differed significantly between Leguminosae and non-Leguminosae, reflecting differences in physiological processes. The negative correlation that we found between regeneration of Leguminosae and N-fixing capacity of isolated trees could be attributed to a loss of the competitive advantage of regenerating Leguminosae in soils of higher N status or to the local abundance of Leguminosae-specific pathogens or pests.

Although our methodological approach does not allow for a formal test of the relative importance of deterministic *versus* stochastic processes (Vellend et al. 2014), it is interesting that the attributes of isolated trees contribute very little to the variation in the model of taxonomic composition while their contribution is notably greater in the models of functional composition, suggesting a stronger determinism of functional composition than taxonomic composition. Several studies of successional woody (Alvarez-Anorve et al. 2012; Muniz-Castro et al. 2012; Swenson et al. 2012; Dent et al. 2013) or grassland (Fukami et al. 2005; Purschke et al. 2013) communities provide evidence of a contrast between the predictability of functional composition and stochasticity of taxonomic and

phylogenetic compositions. Whereas predictable deterministic processes shape the functional composition, the functional redundancy of species (Hubbell 2005) promotes a non-deterministic taxonomic composition depending on a stochastic history of colonization by species in the early stages of succession and on the local species pool. Examining succession through the lens of functional composition rather than taxonomic composition can reveal the deterministic role of resource acquisition and reproduction strategies and therefore promote a better understanding of successional trajectories (Poorter et al. 2004; Lebrija-Trejos et al. 2010b).

Conclusion

Although our study is a snapshot of the early stages of secondary TDF succession, it can inform predictions of longer-term successional trajectories because the regeneration assemblages that we studied will be the origin of future stages, should the pastures be abandoned. Since we observed a correlation between the functional traits of isolated trees and the functional composition of the regeneration assemblage, the species identity of isolated trees present in the pastures is expected to have a long-term effect on the later stages of succession, as observed by Sandor & Chazdon (2014) in humid tropical forest. In other words, these later stages are dependent on the history of colonization (Fukami 2010).

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Supporting Information

Appendix S1. Detailed methods.
Appendix S2. Abundance of species of surveyed regenerating woody plants and isolated trees per site.
Appendix S3. Characteristics of isolated trees and regenerating woody plants.
Appendix S4. Selected models for the number of individuals and the number of species in the regeneration assemblage.
Appendix S5. Selected models for functional composition of the regeneration assemblage.

Table 1. Relationship between landscape factors and properties of the regeneration assemblage in each site. The slope (coefficient) of the GLMs is presented for the model including each landscape factor (explanatory variable) and each of the properties of the regeneration assemblage in turn. Models with $p < 0.001$ are shown as ***, $p < 0.01$ as **, $p < 0.05$ as * and $p > 0.05$ as NS (non-significant). Slope values are only shown for models with $p < 0.05$. The percentage of deviance explained by each model is given in parenthesis as the goodness of fit. *Prop.* is the "proportion of" (*i.e.* the ratio of the number of individuals with the stated trait value : total number of individuals). The proportions of deciduous, compound-leaved and Leguminosae individuals were calculated for the tree and shrub species only; all other results include all regenerating individuals of tree, shrub and liana species.

Landscape factors	Properties of regeneration assemblage						
Site	Number of individuals	Number of species	Prop. trees and shrubs	Prop. zoochorous	Prop. deciduous	Prop. compound-leaved	Prop. Leguminosae
Distance							
Ahogados	-5.169* (10.68)	NS	NS	NS	NS	NS	NS
Aromal	NS	NS	NS	NS	NS	NS	NS
Lamentos	NS	NS	NS	NS	NS	8.760* (25.70)	12.37** (41.54)
$Area_{100}$							
Ahogados	1.341*** (26.88)	0.635** (21.62)	NS	NS	NS	NS	NS
Aromal	NS	NS	NS	NS	NS	NS	NS
Lamentos	NS	NS	NS	-1.587* (26.15)	NS	NS	-2.047*** (52.14)
$Area_{500}$							
Ahogados	NS	NS	NS	NS	NS	-0.055* (16.46)	NS
Aromal	NS	NS	NS	-0.070* (14.56)	NS	NS	NS
Lamentos	NS	NS	NS	NS	NS	-0.075* (27.14)	NS
$Area_{1000}$							
Ahogados	NS	NS	NS	NS	NS	NS	-0.009* (14.56)
Aromal	NS	NS	NS	NS	0.005* (17.40)	NS	NS
Lamentos	NS	NS	NS	NS	NS	-0.049** (34.31)	NS

Table 2. Results of the redundancy analysis (RDA) performed on the taxonomic composition of the woody regeneration assemblage beneath the crowns of 87 isolated trees. Only the significant axes ($p < 0.05$) and the explanatory variables kept in the selected model are presented.

	Axis 1	Axis 2	Axis 3
Percentage of variance accounted for by the explanatory variables	5.00	3.29	2.61
p-value	< 0.001	< 0.001	< 0.001
Canonical coefficients			
Site (Aromal)	-0.0853	-0.2069	0.1293
Site (Lamentos)	0.1897	-0.1915	0.0104
$Area_{100}$	0.0099	0.0428	0.0738
RhH	0.0246	-0.0405	-0.0491
N-fixation (yes)	0.0915	-0.0055	0.0687

Table 3. Results of the selected multiple GLMs between attributes of isolated trees and each of the properties of the regeneration assemblage in turn. *Obs. number* is the number of observations, *i.e.* the number of trees that have been included in the model. The p-value gives the significance of the whole model. *Prop.* is the "proportion of" (*i.e.* the ratio of the number of individuals with the stated trait value : total number of individuals). The proportions of deciduous, compound-leaved and Leguminosae individuals were calculated for trees and shrubs only; all other results include all regenerating individuals of tree, shrub and liana species. Coefficients for which $p < 0.05$ are highlighted. Coefficients with $p < 0.001$ are shown as ***, $p < 0.01$ as **, $p < 0.05$ as * and $p > 0.05$ as NS (non-significant). – indicates variables that have not been kept in the selected model. NA is "not applicable": the variable *Log Sampling area* was tested as a possible covariate only for the models of number of individuals and number of species and the variable *A* only for the models of functional traits of the regeneration assemblage.

	Properties of regeneration assemblage						
	Number of individuals	Number of species	Prop. trees and shrubs	Prop. zoochorous	Prop. deciduous	Prop. compound-leaved	Prop. Leguminosae
Obs. number	88	88	76	77	76	76	76
Explained Deviance (%)	61.10	58.16	21.97	11.16	26.52	12.30	28.96
p-value	<0.001	<0.001	<0.001	0.002	0.002	0.006	<0.001
Coefficients							
Site Aromal	0.653**	0.522***	-0.468***	-	-	-	0.720 **
Site Lamentos	-0.315 NS	-0.312*	-0.036 NS	-	-	-	0.227 NS
Log Sampling area	0.908***	0.404***	NA	NA	NA	NA	NA
Crown area	NA	NA	-	-	-0.001**	-	-0.002 NS
Hbranch	-	-	-	-	-	-	-
RhH	-	-	-	-	1.227*	2.762**	2.637 *
RAh	-	-	-	-	-0.002 NS	-	-
Dispersal (zoochorous)	-	-	-	0.610 **	-	-	-
Phenology (evergreen)	0.227 NS	0.221*	0.131 NS	-	-0.625*	-0.256 NS	-4.614 NS
N-fixation (yes)	-	-	-	-	0.150 NS	-	-0.486 *
Interaction RhH / Phenology	-	-	-	-	-	-	5.696 NS
Interaction RAh / Phenology	-	-	-	-	0.025 NS	-	-

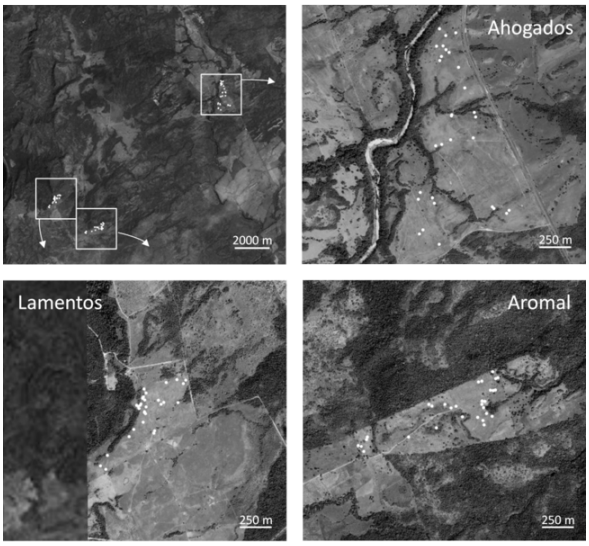

Fig. 1. Positions of the studied pasture sites and trees in the landscape. The upper left panel shows the positions of the three pasture sites (white squares) and the three others show the positions of the studied isolated trees (white dots) within these sites. Orthophoto: ESRI World Imagery - captured in January 2011 (Geoeye, 2011).

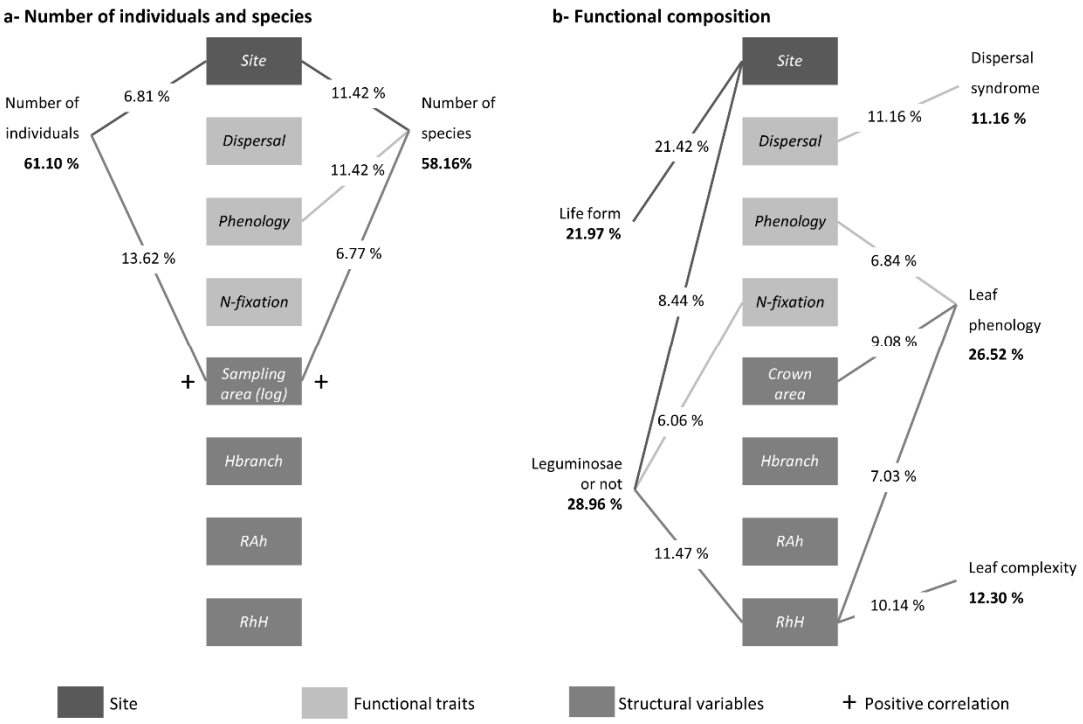

Fig. 2. Relationships between the attributes of isolated trees and the properties of the assemblages of woody plants regenerating beneath their crowns ((a) number of individuals and number of species and (b) functional composition of the regeneration assemblage). The lines link all the significant covariates kept in the best model (attributes of isolated trees, boxes in the centre) with the response variables of this model (properties of the regeneration assemblage) on the sides. The percentage of deviance explained by each model is given in bold below each response variable and the percentage of deviance explained by each isolated tree attribute (deviance explained by the attribute that cannot be explained by any other) in a model is given on the line. The variable *Sampling area* (log-transformed) was tested as a possible covariate only for the models of number of species and number of individuals and the variable *Crown area* only for the models of proportions of functional traits of the regeneration assemblage.